carbon and nutrient budgets allow for greater C costs through increased root respiration in warmer soils[10,29,30] associated with seasonal or climatic increases in temperature. But none of these models or any others that we are aware of make allowance for possible differences in root turnover rates within an ecosystem type, nor are root turnover rates intrinsically linked to soil temperature. We do not wish to imply that current models are flawed in their construction. Instead, they reflect how little is known of the demographic processes (such as root mortality) that control below-ground carbon and nutrient cycling, and the relationship between root demography and the soil environment. Given the importance of fine roots in terrestrial carbon and nutrient budgets[1-10], the need for more and better data on fine root dynamics is apparent. Even if soil temperature is generally found to have a minimal influence on root mortality, the fact that rates of fine root turnover can vary substantially among virtually identical ecosystems needs to be reconciled with current knowledge and models of below-ground processes that do not account for this phenomenon. □

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Increase in C3 plant water-use efficiency and biomass over Glacial to present CO2 concentrations

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ATMOSPHERIC CO_2 concentration was 160 to 200 μmol mol^{-1} during the Last Glacial Maximum (LGM; about 18,000 years ago)[1], rose to about 275 μmol mol^{-1} 10,000 years ago[2,3], and has increased to about 350 μmol mol^{-1} since 1800 (ref. 4). Here we present data indicating that this increase in CO_2 has enhanced biospheric carbon fixation and altered species abundances by increasing the water-use efficiency of biomass production of C_3 plants, the bulk of the Earth's vegetation. We grew oats (*Avena sativa*), wild mustard (*Brassica kaber*) and wheat (*Triticum aestivum* cv. Seri M82 and Yaqui 54), all C3 annuals, and selected C4 grasses along daytime gradients of Glacial to present atmospheric CO_2 concentrations in a 38-m-long chamber. We calculated parameters related to leaf photosynthesis and water-use efficiency from stable carbon isotope ratios ($^{13}C/^{12}C$) of whole leaves. Leaf water-use efficiency and above-ground biomass/plant of C3 species increased linearly and nearly proportionally with increasing CO_2 concentrations. Direct effects of increasing CO_2 on plants must be considered when modelling the global carbon cycle and effects of climate change on vegetation.

The shoots of plants grown in the 38-m chamber were enclosed by a transparent cover through which air was moved in one direction. Photosynthesis by enclosed plants progressively depleted the CO_2 concentration ([CO_2]) and increased the $^{13}C/^{12}C$ of air (B.D.M. *et al.*, manuscript in preparation) as it moved the 38 m from the air intake to outlet of the chamber. The $\delta^{13}C$ values (see Fig. 1 legend) of leaves of C3 species and of concurrently grown C4 grasses, grassbur (*Cenchrus incertus*), crabgrass (*Digitaria ciliaris*) and Gaspé yellow flint maize (*Zea mays*),

were linearly correlated with [CO_2] (Fig. 1). The difference between the $\delta^{13}C$ of atmospheric CO_2 and leaf carbon of maize (and certain other C4 species) is conservative across environments[5] and did not vary significantly with [CO_2] (B.D.M. *et al.*, manuscript in preparation), enabling us to use the $\delta^{13}C$ of C4 leaves as a proxy for the $\delta^{13}C$ of chamber air[6].

Leaf intercellular [CO_2] (c_i), calculated from leaf $\delta^{13}C$ values, increased linearly and nearly proportionally (by the same ratio) with higher ambient [CO_2] (c_a) in each C3 species. As a result, intercellular [CO_2] was a constant but different fraction of c_a in oats ($c_i/c_a = 0.70$) and mustard ($c_i/c_a = 0.65$) grown at mean [CO_2] from 330 to 160 μmol mol^{-1} (Fig. 2). The c_i/c_a of wheat cultivars increased only slightly from 0.63 and 0.66 at 225 μmol mol^{-1} to 0.66 and 0.69 at 350 μmol mol^{-1} for Yaqui 54 and Seri M82, respectively. A similar result has been reported[7] in young wheat plants exposed to CO_2 partial pressures between 120 and 500 μbar. Others have demonstrated that coordination of stomatal and mesophyll functions minimizes variation in c_i/c_a to similar values in C3 species[8], but this is the first demonstration of such for C3 plants grown over a [CO_2] range characteristic of Last Glacial Maximum (LGM)-to-present atmospheric concentrations. Intrinsic water-use efficiency, defined as the ratio of leaf photosynthesis or net assimilation (A) to stomatal conductance to water vapour (g), increased by the same (oats and mustard) or nearly the same (wheat) relative amount as did [CO_2], a consequence of conservative c_i/c_a in these C3 species (Fig. 3).

Leaf assimilation should have increased substantially at the higher c_i that accompanied increasing [CO_2], unless photosynthetic capacity (the relationship of A to c_i) declined. The positive linear relationship of A to c_i at subambient [CO_2] that is typical of C3 species did not differ between oat plants grown at extremes of the [CO_2] gradient[9]. We estimate from that relationship that with a constant c_i/c_a of 0.70, net assimilation of oat leaves would have increased ~40% with the 75 μmol mol^{-1} rise in [CO_2] since 1800. That the increase in leaf c_i was correlated with greater plant carbon gain is evidenced by the positive linear relationships between c_i and aboveground biomass per plant of all C3s studied (Fig. 4).

Climate[10], and particularly site water balance[11], largely control the structure and productivity of vegetation. This control is determined in part by plant water-use efficiency (WUE), biomass produced per unit transpiration. Our results imply that WUE of C3 plants may have increased by 27% over the past 200 years

and ~100% since the LGM. Water-use efficiency calculated from $\delta^{13}C$ is often highly correlated with the ratio of biomass to transpiration of C3 plants[12], but the correlation is influenced by leaf-to-air vapour pressure differences. Little of the CO_2-induced increase in potential WUE might be realized if higher A/g resulted entirely from stomatal closure. Then, transpirational cooling of leaves would decline and leaf temperature and transpiration rate per unit g would rise[13]. Any decline in water loss might also be partly offset by the resulting increase in atmospheric water vapour pressure deficit. But the c_i and biomass/plant of C3 annuals increased by the same ratio as $[CO_2]$, indicating that much of the CO_2-induced increase in A/g (and WUE) was realized as higher A and ultimately as greater plant biomass (Fig. 4). This increase in plant A/g from the LGM to present must have extended the geographic ranges of some

species into areas where precipitation was formerly too low to support growth. We calculate from regression that A/g of oats and mustard would have increased 14.1 to 16.4 mmol CO_2 per mol H_2O, respectively, with the increase from 275 to 350 μmol-mol^{-1} CO_2 that has occurred since 1800. The increase is comparable to the mean 27.6% rise in A/g of 21.9 mmol mol^{-1} of C3 species from moist wash to drier slope habitats in the Sonoran desert, where the change in A/g was associated with a shift in species composition[14].

Our results and those of others[15,16], if representative for C3 species, imply that the rise in $[CO_2]$ since the LGM greatly increased potential productivity of most of Earth's vegetation. Many believe, however, that higher $[CO_2]$ has a negligible effect
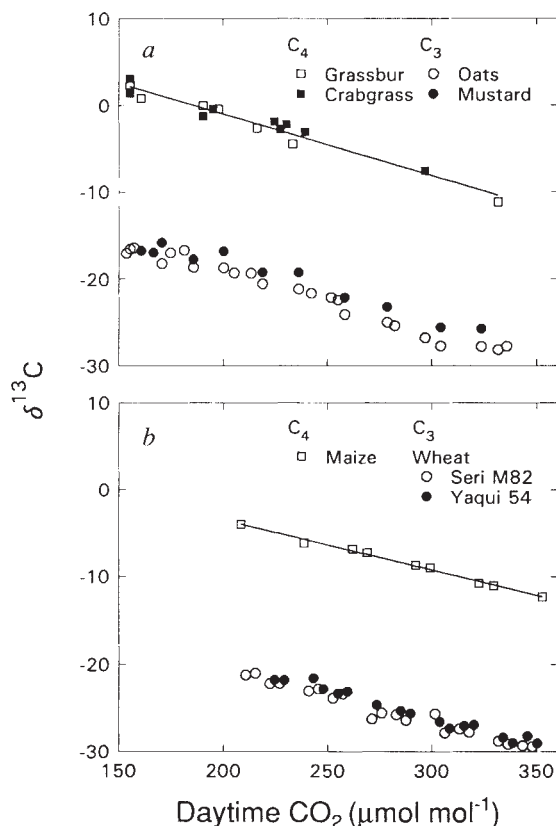

FIG. 1 The stable carbon isotope composition of upper leaves from C3 and C4 plants that were grown at daytime $[CO_2]$ from near 350 μmol mol^{-1} to a, 150 (19 January to 3 May, 1989) or b, 200 μmol mol^{-1} (12 February to 23 May, 1991). The C-isotope composition of whole leaves was determined by mass spectrometry (ISOMASS; VG Isogas) and expressed as $\delta^{13}C$, ‰ (parts per thousand) ^{13}C relative to a PeeDee belemnite reference standard: $\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1] \times 10^3$. Lines are linear regressions of $\delta^{13}C$ of C4 species on mean daytime $[CO_2]$ during growth: $\delta^{13}C = 13.30 - 0.07[CO_2]$, $r^2 = 0.96$, $P < 0.0001$ for grassbur and crabgrass, and $\delta^{13}C = 7.91 - 0.06[CO_2]$, $r^2 = 0.99$, $P < 0.0001$ for maize. Plants were grown from seed in a 38-m long chamber in a ventilated glasshouse[27]. Soil water was restored weekly to field capacity. The chamber consisted of a 0.6-m-high polyethylene cover attached to the top of a 0.76-m-deep and 0.45-m-wide soil container. A desired $[CO_2]$ gradient was maintained in the chamber during daylight (9–10 h daily) by automatically varying the rate of unidirectional air flow through the cover in response to changes in photosynthetic CO_2 depletion by enclosed plants and sunlight intensity. Standard deviation of the minimum daytime $[CO_2]$ was less than 35 μmol mol^{-1} on more than 80% of days. Drybulb and dewpoint temperatures of air were regulated at each 7.6 m along the chamber to track temporal variation in the glasshouse. The daytime drybulb temperature and vapour pressure deficit of air after regulation at each 7.6 m along the chamber were a mean 26°C ($N = 34$) and 1.94 kPa ($N = 33$) during the time sampled leaves of oats and mustard expanded and 20.6 °C ($N = 24$) and 1.13 kPa ($N = 19$) during wheat growth.
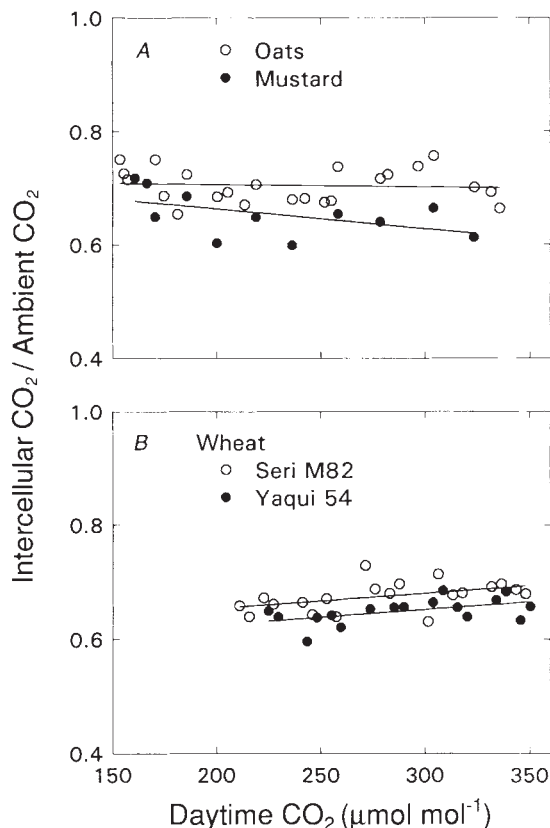

FIG. 2 The ratio of leaf intercellular $[CO_2]$ (c_i) to ambient $[CO_2]$ (c_a), calculated from the $\delta^{13}C$ of leaves, as a function of the daytime $[CO_2]$ at which C3 plants were grown. The slopes of regressions of c_i/c_a on c_a did not differ significantly from zero for (A) oats ($P = 0.70$) or mustard ($P = 0.11$); the c_i/c_a of B, the two wheat cultivars, was positively related to c_a (Seri M82, $c_i/c_a = 0.60 + (2.66 \times 10^{-4})c_a$, $r^2 = 0.22$, $P = 0.04$ and Yaqui 54, $c_i/c_a = 0.57 + (2.71 \times 10^{-4})c_a$, $r^2 = 0.27$, $P = 0.04$). The stable C isotope composition of plants ($\delta p^{13}C$) reflects that of atmospheric CO_2 ($\delta a^{13}C$) and fractionation during photosynthesis[28]. For C3 plants, $\delta p^{13}C = \delta a^{13}C - a - (b - a)c_i/c_a$, where a is a fractionation resulting from the greater diffusivity of $^{12}CO_2$ than $^{13}CO_2$ across leaf stomata (4.4‰; ref. 29); positive values indicate discrimination against ^{13}C or ^{12}C-enrichment) and b is discrimination by ribulose 1,5-bisphosphate carboxylase against ^{13}C in CO_2 fixation (29‰; ref. 30). Leaf c_i/c_a can be deduced from the above equation when $\delta p^{13}C$ and $\delta a^{13}C$ are known. We calculated $\delta_a^{13}C$ as a function of c_a in the 38-m chamber from the $\delta^{13}C$ of leaves from C4 plants that were grown with oats, mustard and wheat using a fractionation by C4 plants relative to air of 3.136 ‰. Isotope fractionation by maize grown across a 350–200 μmol mol^{-1} CO_2 gradient in an additional experiment did not vary significantly with $[CO_2]$ ($\bar{x} = 3.136$‰, s.e. $= 0.06$‰, $N = 9$; B.D.M. et al., manuscript in preparation). Regressions of $\delta^{13}C$ on daytime $[CO_2]$ did not differ significantly for grassbur and crabgrass grown with oats and mustard (Fig. 1a; $F_{(2,12)} = 2.6$, $P < 0.10$) or for maize and crabgrass grown with wheat (data not shown; $F_{(2,29)} = 2.7$, $P > 0.10$). The small changes in drybulb and dewpoint temperatures between points of regulation at each 7.6 m along the chamber[9] had no significant influence on the relationship of c_i/c_a of individual species or cultivars to c_a.

on global carbon fixation because factors other than CO_2 limit productivity of most unmanaged vegetation[17,18]. Some recent research suggests that a step increase in [CO_2] above the current 350 μmol mol^{-1} produces little or no short-term ($\leqslant 3$ years) increase in plant or ecosystem carbon storage where low temperatures or nutrient (particularly nitrogen) availability currently restrict plant growth[19,20]. Extrapolation from these studies to the past is difficult, for only superambient [CO_2] and a limited range of processes and temporal scales were considered. Plant water- and light-use efficiencies[21] were lower at subambient [CO_2], implying that sustainable biomass and plant nutrient requirements were also lower in the past. Species and genetic change, fixation of atmospheric N_2, and nitrogen deposition may have facilitated plant response to CO_2 in the past when concentrations rose more slowly or with a greater relaxation time between change than today, but data are lacking.

Increased widths of annular rings of some trees[22], global CO_2 models[23], calculations of carbon accumulation in temperate forests[24], and the increased amplitude of the annual cycle of atmospheric [CO_2][25] in recent decades, all suggest that rising [CO_2] has stimulated biospheric carbon fixation. Effects of [CO_2], however, cannot readily be distinguished from those of human impact and concurrent climate change[24]. Resolution of what fraction has been realized, if any, of the potentially great increase in plant productivity since the LGM demands that effects of [CO_2] on the processes that influence plant growth be

FIG. 4 Relationships of above-ground biomass per C3 plant at maturity to leaf intercellular [CO_2] (c_i). Leaf c_i was determined from the stable C isotope composition of plants grown from current atmospheric [CO_2] to a, near 150 μmol mol^{-1} (oats, mustard; 20 plants per m^2) or b, 200 μmol mol^{-1} CO_2 (wheat; 350 plants m^{-2}). Note that the scale of the ordinate differs in a and b. Lines are linear regressions of above-ground biomass per plant on leaf c_i: biomass $= -4.42 + 0.10 c_i$ for oats ($N = 19$) and biomass $= -6.00 + 0.17 c_i$ for mustard ($N = 11$), $r^2 = 0.58$, $P < 0.01$ and biomass $= -0.63 + 0.01 c_i$, $r^2 = 0.81$ and biomass $= -0.62 + 0.01 c_i$, $r^2 = 0.77$ for Seri M82 and Yaqui 54 cultivars of wheat, respectively, $P < 0.001$, $N = 10$.

understood within an ecosystem context and over relevant periods. Our results nonetheless demonstrate the risks inherent in using present vegetation–climate relationships to reconstruct past climates from pollen or fossil records without incorporating potential direct effects of [CO_2][26]. □
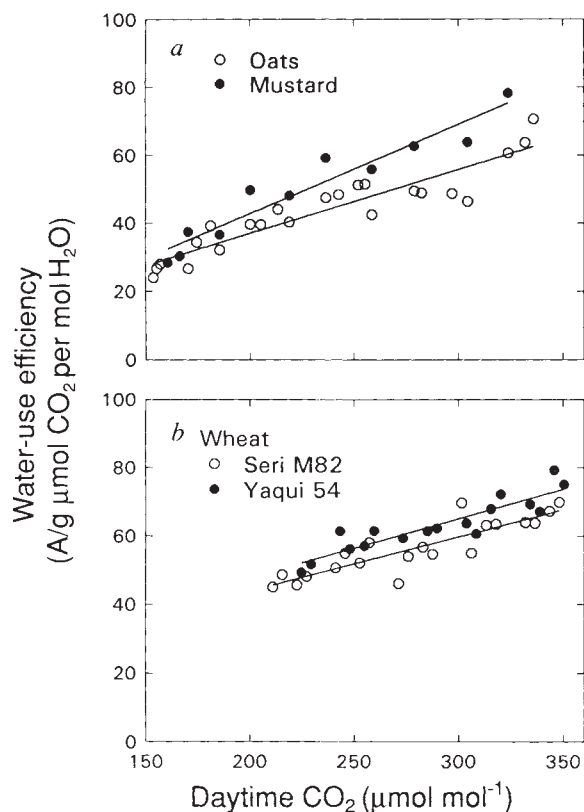

FIG. 3 Relationships between intrinsic water-use efficiencies of C3 plants (net assimilation (A)/stomatal conductance to water (g)) derived from the δ^{13}C of leaves and the daytime [CO_2] (c_a) at which plants were grown. Linear regressions differed significantly ($P < 0.005$) between a, oats ($A/g = -0.70 + 0.19 c_a$, $r^2 = 0.86$) and mustard ($A/g = -9.91 + 0.26 c_a$, $r^2 = 0.92$), and b, two cultivars of wheat, Seri M82 ($A/g = 12.05 + 0.16 c_a$, $r^2 = 0.77$) and Yaqui 54 ($A/g = 13.29 + 0.17 c_a$, $r^2 = 0.82$). $P < 0.0001$ for each regression. Intrinsic water-use efficiency of C3 leaves is directly proportional to c_a and negatively correlated with the ratio of leaf intercellular [CO_2] (c_i) to c_a: $A/g = c_a (1 - c_i/c_a)/1.6$, where 1.6 is the ratio of gaseous diffusivities of CO_2 and water vapour in air. The c_i/c_a was determined from the stable C isotope compositions of leaves.
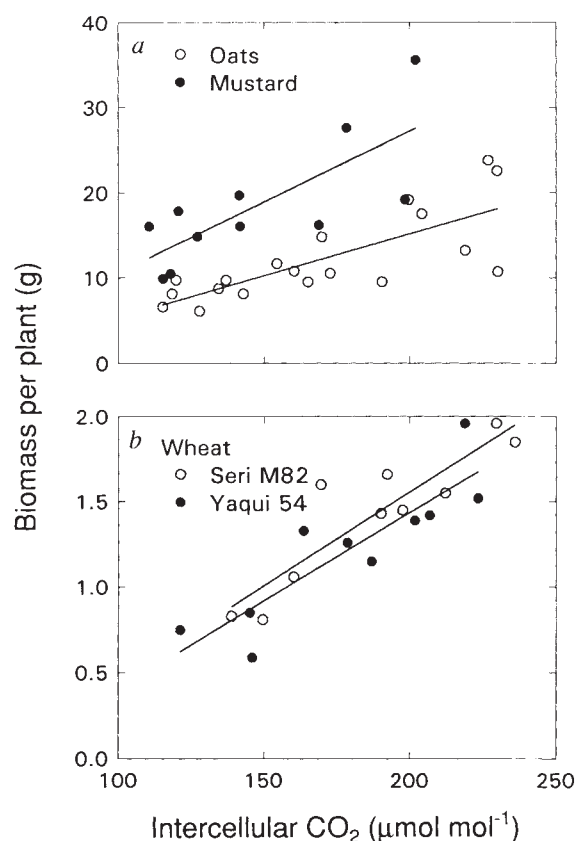
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Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria

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WE report here the discovery of a primitive dinosaur skeleton from Upper Triassic strata in northwestern Argentina. The 1-m-long skeleton represents a new taxon, *Eoraptor lunensis* gen. et sp. nov., which is close to the predicted structure and size of the common dinosaurian ancestor[1–5]. The skull, which has a unique heterodont dentition, does not exhibit any of the specializations of the major dinosaurian clades (Ornithischia, Sauropodomorpha, Theropoda). The forelimbs are less than half the length of the hind limbs, which suggests an obligatory bipedal posture. Although close in overall form to the common dinosaurian ancestor, the functionally tridactyl, grasping/raking hand and other features show that *Eoraptor* is allied phylogenetically with theropods. The discovery of *Eoraptor* supports the hypothesis that dinosaurs diverged rapidly at small body size from a common ancestor, with the

principal herbivorous and carnivorous lineages present by the middle Carnian.

Skeletal remains of the earliest (middle Carnian) dinosaurs are rare and have been unearthed mostly from the fossiliferous Upper Triassic Ischigualasto Formation in northwestern Argentina. These dinosaurs include the ornithischian *Pisanosaurus*[6] and the theropod *Herrerasaurus*[1,7–9]. The new skeleton, a contemporary of *Herrerasaurus* in the lower third of the formation (R.R.R., C. C. Swisher, P.C.S., C.A.F. and A.M.M., manuscript in preparation), represents a third species. Despite its small size, closure of sutures in the vertebral column and partial fusion of the scapulocoracoid suggest that the skeleton had reached adult size.

Order Saurischia

Suborder Theropoda

Eoraptor lunensis gen. et sp. nov.

Etymology. *Eos,* dawn (Greek) in reference to its primitive structure and early temporal occurrence; *raptor,* plunderer (Latin) in reference to its carnivorous habits and grasping hand; *luna,* moon (Latin) and *-ensis,* place (Latin), in reference to the type locality.
Holotype. PVSJ 512 (Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina), an articulated skeleton lacking only the distal caudal vertebrae (Figs 1 and 2). The skeleton was preserved in a muddy siltstone in close association with many of the common vertebrates in the Ischigualasto fauna (*Herrerasaurus, Saurosuchus, Aetosauroides, Ischigualastia, Exaeretodon,* and an undescribed small carnivorous cynodont).
Horizon and locality. Ischigualasto Formation (Upper Triassic: middle Carnian); Valley of the Moon (Ischigualasto Provincial Park, Ischigualasto-Villa Unión Basin, northwestern Argentina) (R.R.R. *et al.,* manuscript in preparation).
Diagnosis. Small 1-m-long theropod with external naris slightly enlarged, premaxilla with slender posterolateral process, and leaf-shaped premaxillary and anterior maxillary crowns.

The skull follows a primitive saurischian design, with transversely narrow proportions, a relatively large antorbital opening, a small subnarial foramen beneath the external naris, and a forked posterior process on the jugal (Fig. 1*a, b*). Derived cranial characters that distinguish ornithischians, sauropodomorphs, and theropods, however, are absent. For example, there is no
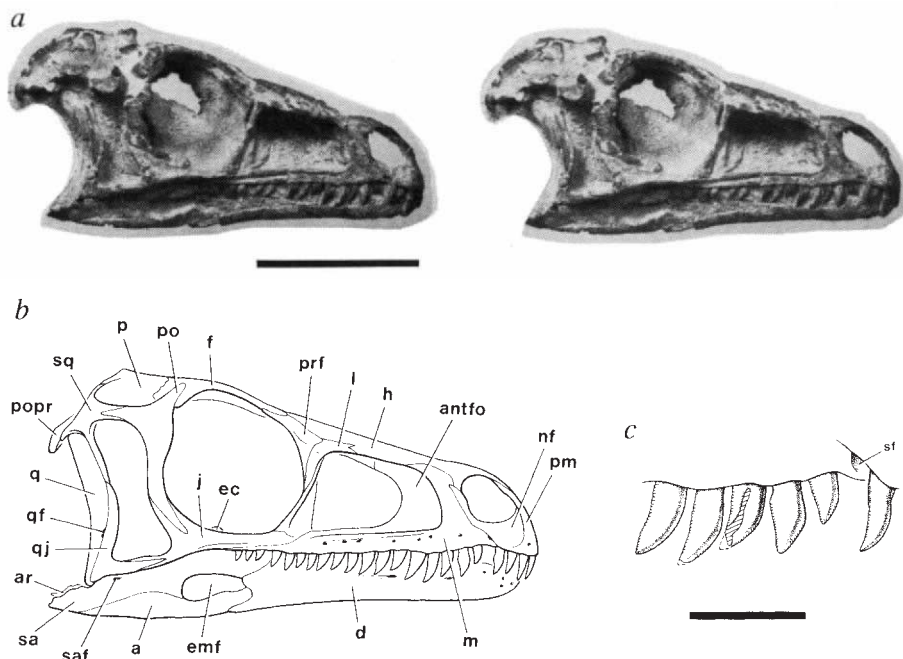

FIG. 1 PVSJ 512, *Eoraptor lunensis,* new species. *a,* Stereopair and *b,* reconstruction of the skull in right lateral view. *c,* Right posterior premaxillary and anterior maxillary teeth in lateral view. Abbreviations: a, angular; antfo, antorbital fossa; ar, articular; d, dentary; emf, external mandibular fenestra; ec, ectopterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; nf, narial fossa; p, parietal; pm, premaxilla; po, postorbital; popr, paroccipital process; prf, prefrontal; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; saf, surangular foramen; sf, subnarial foramen; sq, squamosal. Scale bar, *a,* 5 cm; *c,* 1 cm.